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The fossil crown wasp *Electrostephanus petiolatus* Brues in Baltic Amber (Hymenoptera, Stephanidae): designation of a neotype, revised classification, and a key to amber Stephanidae

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Abstract

The fossil crown wasp *Electrostephanus petiolatus* Brues **comb. rev.** (Stephanidae, Electrostephaninae) is redescribed from a single male preserved in middle Eocene Baltic Amber. The holotype was lost or destroyed around the time of World War II and subsequent interpretations of its identity have been based solely on the brief descriptive comments provided by Brues in his original account. The new specimen matches the original description and illustration provided by Brues in every detail and we hereby consider them to be conspecific, selecting the specimen as a neotype for the purpose of stabilizing the nomenclature for this fossil species. This neotype exhibits a free first metasomal tergum and sternum, contrary to the assertion of previous workers who indicated these to be fused. Accordingly, this species does indeed belong to the genus *Electrostephanus* Brues rather than to *Denaeostephanus* Engel & Grimaldi (Stephaninae). *Electrostephanus petiolatus* is transferred to a new subgenus, *Electrostephanodes* **n. subgen.**, based on its elongate pseudopetiole and slender gaster, but may eventually warrant generic status as the phylogenetic placement of these fossil lineages continues to be clarified. A revised key to the Baltic amber crown wasps is provided.

Keywords

Hymenoptera, Stephanomorpha, Stephanoidea, Stephanidae, Electrostephaninae, *Electrostephanus*, neotype, taxonomy, Tertiary, Eocene, amber

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Introduction

The crown wasps (Stephanidae) occupy a distinguished position among the diversity of parasitoid Hymenoptera (Euhymenoptera). The family is the basalmost living lineage of apocritan wasps, representing the sole survivors of the initial diversification of Apocrita (e.g., Rasnitsyn, 1975, 1980; Königsmann, 1978; Whitfield, 1992, 1998; Vilhelmsen, 1996, 2001; Grimaldi and Engel, 2005). Despite their apparent antiquity, fossil stephanids are rare and of relatively recent age. The oldest definitive stephanid is *Archaeostephanus corae* Engel & Grimaldi, a schlettereriine in Late Cretaceous (Turonian) amber from New Jersey (Engel and Grimaldi, 2004). All other records of stephanids are from the Tertiary and largely from the middle Eocene or Eocene-Oligocene boundary. The youngest and also the first discovered stephanid fossil is *Protostephanus ashmeadi*, described by Cockerell (1906) from a single female preserved as a compression with little relief from the Florissant shales in Colorado, USA. The remaining Tertiary species are all preserved as inclusions in middle Eocene (Lutetian) amber from the Baltic region. Brues (1933) described three species, assigning them to the extinct genus *Electrostephanus* Brues. Subsequently Aguiar and Janzen (1999) discussed two new species, placing them in Brues's genus and simultaneously attempting to evaluate Brues's taxa. Engel (2005) later reported the discovery of the first female for *Electrostephanus* based on males and females of a new species, the material serving to clarify the placement of the genus as sister to but distinctly outside of the Stephaninae. To date these represent our sole insights into the geological past of one of the most phylogenetically and biologically interesting parasitoid wasp families.

Herein we report the discovery of a new male crown wasp in Baltic amber. The new specimen is identical with the male described by Brues (1933) as *Electrostephanus petiolatus*. Brues's holotype was in the Albertus Universität, Königsberg collection which was largely destroyed by fire during the bombings of World War II. Some material from this important collection does survive to this day in the Institut und Museum für Geologie und Paläontologie, Göttingen and a few specimens have turned up in other locations [e.g., the rediscovery of the holotype of the gall wasp *Aulacidea succinea* Kinsey (now *Kinseycynips succinea*) in the Kinsey Collection at the American Museum of Natural History: Liu et al., 2007]. However, a personal examination of the Göttingen material by the senior author in July 1999 recovered no specimen of *Electrostephanus*. Accordingly we have selected the new specimen as a neotype in order to stabilize the application of the names for fossil stephanids and provided a clarification of its identity.

Material and methods

The specimen reported herein is from the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History (AMNH), New York and was formerly part of the Jens-Wilhelm Janzen Collection of Baltic amber Hymenoptera. For the description the format follows that of Engel (2005), with the morphological terminology following that used elsewhere for crown wasps (e.g., Aguiar and Janzen, 1999; Achterberg, 2002; Engel, 2005).

Systematic paleontology

Family Stephanidae Leach, 1815
Subfamily Electrostephaninae Engel, 2005
Genus *Electrostephanus* Brues, 1933

Subgenus *Electrostephanodes* Engel & Ortega-Blanco, subgen. n.
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Type species. *Electrostephanus petiolatus* Brues, 1933.

Diagnosis. *Male*: Body of moderate-size (ca. 9 mm); slender. Antenna with more than 20 articles (23 in type species). Metacoxa without dorsal tooth; ventral surface of metafemur with three principal teeth, one blunt tooth near base, one larger blunt tooth near midlength, and one blunt tooth near apex, with seven minor, blunt teeth between principal teeth; tarsi pentamerous; pretarsal ungues simple; arolium present. Forewing with long, arched basal vein; vein $Rs+M_b$ absent; bullae absent; $2Cu_a$ and $2Cu_b$ present and tubular; 2A, 3A, and 2cu-a nebulous; hind wing with only Sc+R present. First metasomal terga and sterna elongate, about five times longer than wide, but distinctly separate (not fused as in Stephaninae, such as *Denaeostephanus* Engel & Grimaldi, also in Baltic amber), thus forming "pseudo-petiole", pseudo-petiole nearly as long as mesosoma; gaster slender, not distinctly thickened relative to pseudo-petiole, width gently tapering along its length. *Female*: Unknown.

Etymology. The new genus-group name is a combination of *Electrostephanus* and an adjectival derivative of *eidos* (Greek, meaning, "kind" or "having the form of"). The name is masculine (while generic words ending in the noun *eidos* are neuter, those ending in the adjectival derivatives, such as *–odes* or *–oides*, may be in practice any gender [masculine, feminine, or neuter]: Brown, 1954).

Electrostephanus (Electrostephanodes) petiolatus* Brues, *combinatio revivisco

Electrostephanus petiolatus Brues, 1933: 14 [holotype male, in ill-fated Königsberg Collection, presumed destroyed]; Aguiar and Janzen, 1999: 444 [key]; Achterberg, 2002: 12 [mentioned in Schlettereriinae]; Aguiar, 2004: 14 [catalogue].

Denaeostephanus petiolatus (Brues), Engel and Grimaldi, 2004: 1194 [tentative transfer to genus based on description of petiole by Aguiar and Janzen (1999)]; Engel, 2005: 318 [mentioned].

Type material. Neotype (**here designated**) male; AMNH B-JWJ-260, Baltic amber, Eocene (Lutetian), and labeled "Neotype, *Electrostephanus petiolatus* Brues, desig. Engel & Ortega-Blanco [red label]". Formerly part of the Jens-Wilhelm Janzen collection.

Diagnosis. As for the subgenus (*vide supra*).

Description. *Male*: Total body length (from head anterior margin to metasoma posterior margin) 9.84 mm; forewing length (from tegula to apex) 5.04 mm. Integument dark brown to black (where evident) with scattered, thin, simple, erect or suberect setae as noted. Head globular, with compound eyes occupying around one-half of lateral surface, eyes well separated from preoccipital area; "crown" composed of 5 tubercles arising anterior to series of four transverse carinae between lateral ocelli around compound eyes, median ocellus set just anterior to series of carinae; tubercles arranged with anteriormost tubercle medial on frons, lateral tubercles paired in longitudinal series parallel to compound eye; integument of face rugulose, integument posterior to carinae and on gena impunctate and smooth. Antennae with 23 articles, arising from clypeus boundary at about compound eye midlength; scape about twice as long as wide, somewhat ovoid, surface bordering malar space slightly flattened; pedicel about one-half scape length, almost as wide as long; first flagellomere as long as pedicel but one-half width; second flagellomere around four times longer than wide, slightly less than twice length of first flagellomere; third through fifth subequal in length and shape; remaining flagellomeres progressively shorter, except apicalmost flagellomere with tapered apex. Maxillary palpus 5-segmented, elongate, elbowed between MP_2 (maxillary palpomere II) and MP_3, MP_1 and MP_2 thicker than $MP_{3–5}$, MP_1 shortest, MP_2 about twice length of MP_1, MP_3 slightly less than twice length of MP_2, MP_4 and MP_5 equal in length to MP_3. Labial palpus short, apparently 3-segmented (base obscured), slightly widening apically except LP_3 with acutely pointed apex.

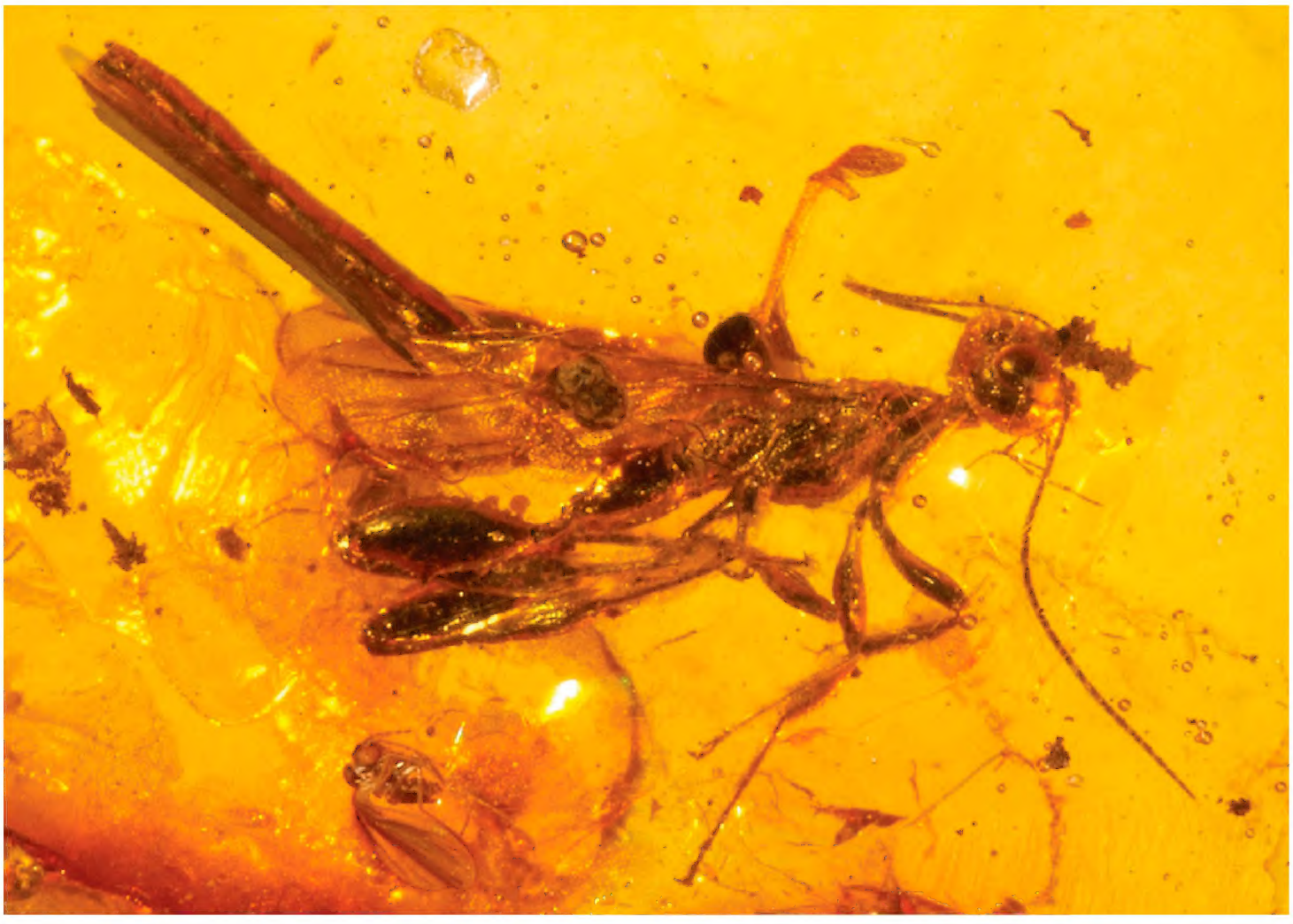

Fig. 1. Neotype male of *Electrostephanus petiolatus* Brues in Baltic amber (AMNH B-JWJ-260).

Pronotum long, transversely striate along neck, near articulation with head, remainder of surface imbricate and irregular, laterally and dorsoventrally micro-rugulose, posterior portion with sparse, erect, long, simple setae; propleuron finely imbricate, with scattered shallow punctures. Mesoscutum, mesoscutellum, and metanotum apparently largely imbricate, with scattered shallow punctures (direct view of this surface slightly obscured), with sparse, erect, long, simple setae; pleura largely coarsely and irregularly punctured, punctures deep, large, and nearly contiguous, forming irregular network, except posterior half of mesopleuron with large, impunctate and imbricate area bordered posteriorly by dorsoventral column of coarse, large, punctures along boundary with metapleuron; metapleuron with longitudinal series of irregular rugae, posteriorly with coarse, irregular, contiguous punctures like those on anterior portion of mesopleuron except more deeply impressed.

Pro- and mesocoxae short and cylindrical, imbricate; metacoxa massive, wider at base, oriented posteriorly, imbricate except basally somewhat rugose; trochanters narrow at base, gently and slightly widening apically, with distinct trochantellus; femora finely imbricate; pro- and mesofemora with proximal thirds narrowly petiolate; metafemur fusiform, widest at mid-point; ventral surface of metafemur with a blunt, triangular, principal tooth at first third of length, a more acute and longer tooth near midlength, and a tooth near apex in apical third of length; three minor teeth or protuberances between medial tooth and others, such protuberances slightly closer to medial tooth, another protuberance just prior to distalmost principal tooth; a thin, long seta arising from each protuberance; metafemur with scattered, erect, long, slightly fuscous setae; tibiae finely imbricate, thin and elongate, with nearly basal halves narrowly petiolate, with a row of short spines on anterior and posterior surfaces of pro- and mesotibia; metatibia with several long setae at apex, inner surface with thin patch of microtrichia; tibial spurs 1-2-2, stout and short; metabasitarsus with a row of stouter setae anteriorly and posteriorly; remaining tarsomeres with two distinct long, thick distal setae; tarsal relative proportions – (all in comparison to associated basitarsus = 1) foreleg: 1 : 0.5 : 0.3 : 0.3 : 0.4; midlegs: 1 : 0.4 : 0.4 : 0.3 : 0.4; hind legs: 1 : 0.4 : 0.25 : 0.8 : 0.5; fourth tarsomere with distal ventral surface elongate, extending under most of fifth tarsomere; fifth tarsomere arising from near midlength of fourth tarsomere; pretarsal ungues (= claws) long, curved, and simple.

Wing membranes hyaline. Forewing with parallel-sided, dark brown pterostigma, slightly more than three times longer than high; Rs apex not reaching completely wing margin but extending well beyond pterostigma, demarcating a long, open marginal cell; basal vein (first free abscissa of M) arched proximally along basal half, about three times as long as first free abscissa of Rs, about twice 1m-cu length and approximately parallel to 1m-cu, demarcating a trapezoidal medial cell (= discal cell); $Rs+M_b$ and bullae absent; submarginal cell pentagonal, wider apically, r-rs slightly less than one-half length of second free abscissa Rs; cubital cell rectangular, three times longer than high; M and Cu almost reaching wing margin as nebulous veins; 3A, 2cu-a, and apical third of 2A nebulous; posterior margin of wing with very short, thin setae. Hind wing with four distal hamuli; only Sc+R present, thin and tubular.

Metasoma slender, elongate, terga and sterna not fused laterally, integument finely imbricate except pseudo-petiole rugulose, sternum with irregular transverse rugae ba-

sally; first metasomal tergum and sternum forming a narrow, tubular pseudo-petiole (a "true" petiole in Stephanidae have the tergum and sternum fused laterally), about five times longer than wide; metasomal segments II–V subequal in length, remaining terga progressively shorter, second and third metasomal segments about three times longer than wide; gastral terga with exceptionally sparse setae, setae suberect, simple and long; gastral sterna with sparse, erect or suberect, elongate setae; parameres exposed, broad, tapering gradually to bluntly rounded apices, with fringe of dense, erect, moderate-length, slightly fuscous setae at apex.

Female: Unknown.

Discussion

Aguiar and Janzen (1999) presented a key to the species of *Electrostephanus*, *sensu* Brues (1933), and noted at that time that *E. petiolatus* had the first metasomal tergum and sternum fused to form a long, tubular petiole like *E. tridentatus* Brues and *E. sulcatus* Aguiar & Janzen. Engel and Grimaldi (2004) noted that the condition of a fused tergum and sternum was derived and indicated a relationship closer to typical Stephaninae, while the plesiomorphic free condition was similar to that retained in the subfamily Schlettereriinae. Accordingly, those species with the first metasomal tergum and sternum fused were transferred to the genus *Denaeostephanus*, and based on the assertion by Aguiar and Janzen (1999) that *E. petiolatus* was of this form the species was tentatively placed therein as *Denaeostephanus petiolatus* (Brues).

The new specimen reported herein is immediately recognizable as *E. petiolatus* based on the form of the male metasoma. Indeed, the specimen matches all those traits described by Brues (1933) except that the overall size is slightly larger, the base of the pterostigma does not appear lighter ("pale" basally according to Brues but uniformly brown in the new specimen, likely differences in preservation as color is often off in Baltic amber specimens), and the pterostigma is about 3.5 times longer than high rather than merely thrice as long as high. All of these are very minor differences and may either be due to preservation (coloration of pterostigma) or be associated with variations in size. While the species was considered to have a more derived petiole, like Stephaninae, the petiolar tergum and sternum are clearly separate. Although the wings obscure some of the view of the metasomal base, the lateral surface of the first metasomal segment can be clearly seen in left lateral aspect (and from a slightly ventrally oblique view) where a clear separation between the sclerites is observed. This is a remarkable feature in that the species retains the primitively separate first metasomal tergum and sternum while possessing the more elongate form (nearly as long as the mesosoma) of many other genera. Given this revelation, the assignment of *E. petiolatus* to *Denaeostephanus* (Stephaninae) is no longer founded and the species is returned to *Electrostephanus* and the Electrostephaninae.

Brues placed his three fossil species in a single, extinct genus based on their relatively low number of antennal articles in comparison to modern stephanids, but noted that other features of importance were heterogeneous among his species (e.g., the formation of

the petiole). As such, his grouping was not natural and reflected more the notion that the species were primitive and were in Baltic amber (i.e., the genus was named more for the fauna rather than the phylogenetic affinities of the individual taxa). Accordingly, the genus was unnatural in composition and, not surprisingly, the fauna was more heterogeneous in lineages represented than Brues's classification implied. This was also noted correctly to some degree by Aguiar and Janzen (1999), although in the absence of more material, particularly females, they chose to follow Brues's system of considering all Baltic amber species as "*Electrostephanus*". Engel and Grimaldi (2004) and Engel (2005) attempted to more accurately represent the phylogenetic heterogeneity of the fauna by segregating the primitive *Electrostephanus* from the clearly derived *Denaeostephanus*, the latter belonging to the Stephaninae. We have here further highlighted the diversity of these species by segregating *E. petiolatus* into a distinct subgenus relative to its congeners. The elongate pseudopetiole, tapered gaster, and more elongate antenna of *E. petiolatus* are derived features relative to other *Electrostephanus*. Indeed, *Electrostephanodes* could warrant generic status but we have hesitated from fully pulling the species out of *Electrostephanus* until more material is located (the current supraspecific classification of the family is summarized in table 1).

Table 1. Supraspecific classification of living and fossil crown wasps (Stephanidae) (updated from Engel, 2005).

Family STEPHANIDAE Leach
- Subfamily Schlettereriinae Orfila
  - Genus †*Archaeostephanus* Engel & Grimaldi
  - Genus *Schlettererius* Ashmead
- Subfamily †Electrostephaninae Engel
  - Genus †*Electrostephanus* Brues
    - Subgenus †*Electrostephanodes* Engel & Ortega-Blanco **n. subgen.**
    - Subgenus †*Electrostephanus* Brues
- Subfamily Stephaninae Leach
  - Genus †*Protostephanus* Cockerell
  - Genus †*Denaeostephanus* Engel & Grimaldi
  - Tribe Stephanini Leach
    - Genus *Stephanus* Jurine
  - Tribe Megischini Engel & Grimaldi
    - Genus *Hemistephanus* Enderlein
    - Genus *Megischus* Brullé
    - Genus *Pseudomegischus* Achterberg
      - Subgenus *Pseudomegischus* Achterberg
      - Subgenus *Callomegischus* Achterberg
  - Tribe Foenatopodini Enderlein
    - Subtribe Madegafoenina Engel & Grimaldi
      - Genus *Madegafoenus* Benoit
      - Genus *Afromegischus* Achterberg
    - Subtribe Foenatopodina Enderlein
      - Genus *Parastephanellus* Enderlein
      - Genus *Comnatopus* Achterberg
      - Genus *Profoenatopus* Achterberg
      - Genus *Foenatopus* Smith

Electrostephanus neovenatus Aguiar & Janzen is another enigmatic species, primitively retaining the separated and short first and second metasomal terga, but with a more derived wing venation. Unfortunately, the antennae are incomplete in the holotype and it is difficult to ascertain at this time whether it should be segregated into its own genus. Hopefully more completely preserved material will be recovered and the species elaborated upon.

Based on the wealth of new information available for *E. petiolatus* we provide here a revised key to the Baltic amber species of Stephanidae.

Revised key to Baltic Amber Stephanidae

1 First metasomal tergum and sternum fused laterally to form distinct petiole (*Denaeostephanus* Engel & Grimaldi) 2

– First metasomal tergum and sternum not fused, separated by small membranous area ("pseudo-petiole") (*Electrostephanus* Brues) 3

2 Metafemur with two principal teeth, one near midlength and one near apical quarter ..... *D. sulcatus* (Aguiar & Janzen)

– Metafemur with three principal teeth, one near proximal quarter, one near midlength, and one near apex ..... *D. tridentatus* (Brues)

3 Forewing vein $Rs+M_b$ absent or scarcely present; bullae absent 4

– Forewing vein $Rs+M_b$ distinctly present; bullae present ..... *E. neovenatus* Aguiar & Janzen

4 Forewing $2Cu_a$ and $2Cu_b$ absent or nebulous; $Rs+M_b$ absent or scarcely present; pseudo-petiole short, one-half mesosomal length or less; gaster relatively robust, distinctly thicker than pseudo-petiole; metafemur with two principal teeth, one near midlength, one near apex; antenna with fewer than 20 articles; smaller species, males 4–7.1 mm in length 5

– Forewing $2Cu_a$ and $2Cu_b$ present and tubular; $Rs+M_b$ absent; petiole elongate, nearly as long as mesosoma; gaster slender, tapering gradually from pseudo-petiole to apex; metafemur with three principal teeth, one proximally, one near midlength, one near apex; antenna with 23 articles; larger species, males 9.0–10.0 mm in length (subgenus *Electrostephanodes* **n. subgen.**) ..... *E. petiolatus* Brues

5 Male antenna with 14 articles; second through fourth flagellar articles each widened apically and about three times longer than wide; forewing $Rs+M_b$ scarcely present (exceedingly short), $2Cu_a$ and $2Cu_b$ nebulous; moderate-sized species, males 6.0–7.1 mm in length ..... *E. janzeni* Engel

– Male antenna with 17 articles; second and third flagellar articles each widened apically and 2.5 times longer than wide, fourth flagellar article not widened apically and three times longer than wide; forewing $Rs+M_b$, $2Cu_a$, and $2Cu_b$ absent; smaller species, male 4.2 mm in length ..... *E. brevicornis* Brues

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References

Achterberg C van (2002) A revision of the Old World species of *Megischus* Brullé, *Stephanus* Jurine and *Pseudomegischus* gen. nov., with a key to the genera of the family Stephanidae (Hymenoptera: Stephanoidea). Zoologische Verhandelingen 339: 1-206.

Aguiar AP (2004) World catalog of the Stephanidae (Hymenoptera: Stephanoidea). Zootaxa 753: 1-120.

Aguiar AP, Janzen J-W (1999) An overview of fossil Stephanidae (Hymenoptera), with description of two new taxa from Baltic amber, and key to species of *Electrostephanus* Brues. Entomologica Scandinavica 30(4): 443-452. [Publication date: January 2000]

Brown RW (1954) Composition of Scientific Words: A Manual of Methods and a Lexicon of Materials for the Practice of Logotechnics. Smithsonian Institution Press, Washington.

Brues CT (1933) The parasitic Hymenoptera of the Baltic amber. Part 1. Bernstein Forschungen 3: 4-178.

Cockerell TDA (1906) Fossil Hymenoptera from Florissant, Colorado. Bulletin of the Museum of Comparative Zoology 50(2): 33-58.

Engel MS (2005) The crown wasp genus *Electrostephanus* (Hymenoptera: Stephanidae): Discovery of the female and a new species. Polskie Pismo Entomologiczne 74(3): 317-332.

Engel MS, Grimaldi DA (2004) The first Mesozoic stephanid wasp (Hymenoptera: Stephanidae). Journal of Paleontology 78(6): 1192-1197.

Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, Cambridge.

Königsmann E (1978) Das phylogenetische System der Hymenoptera. Teil 3: "Terebrantes" (Unterordnung Apocrita). Deutsche Entomologische Zeitschrift 25: 1-55.

Leach WE (1815) Entomology. In: Brewster D (Ed) The Edinburgh Encyclopædia [Vol. 9 (part 1)]. Blackwood, Edinburgh, 57-172.

Liu Z, Engel MS, Grimaldi DA (2007) Phylogeny and geological history of the cynipoid wasps (Hymenoptera: Cynipoidea). American Museum Novitates 3583: 1-48.

Rasnitsyn AP (1975) Hymenoptera Apocrita of the Mesozoic. Transactions of the Paleontological Institute, Academy of Sciences, USSR 147: 1-132. [In Russian]

Rasnitsyn AP (1980) An outline of evolution of the hymenopterous insects (order Vespida). Oriental Insects 22: 115-145.

Vilhelmsen L (1996) The preoral cavity of lower Hymenoptera (Insecta): Comparative morphology and phylogenetic significance. Zoologica Scripta 25(2): 143-170.

Vilhelmsen L (2001) Phylogeny and classification of the extant basal lineages of the Hymenoptera (Insecta). Zoological Journal of the Linnean Society 131(4): 393-442.

Whitfield JB (1992) Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera. Journal of Hymenoptera Research 1: 3-14.

Whitfield JB (1998) Phylogeny and evolution of host-parasitoid interactions in Hymenoptera. Annual Review of Entomology 45: 129-151.